

Diversity of trichomes from mature cypselar surface of some taxa from the basal tribes of Compositae

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Abstract

Structure and distribution of trichomes are important from the taxonomic point of view. The distribution and structure of trichomes appear to be genetically controlled and are more or less stable and have paramount taxonomic significance.

It has been observed by many workers that trichomes from the vegetative as well as reproductive parts can be used successfully for the delimitation of genera and species within the family Compositae (Asteraceae). However, broad comparative studies of cypselar trichomes are scarce or lacking. The present study indicates that trichome structure is highly variable. Trichomes from the outer surface of mature cypselas of 44 genera and 71 species belonging to 7 tribes of the four subfamilies Mutisioideae, Carduoideae, Pertyoideae and Cichorioideae were studied by light microscopy and SEM. Number of studied genera and species in each tribe is indicated in parentheses: Mutisieae (1/3), Dicomeae (1/1), Cardueae (9/17), Pertyeae (1/3), Cichorieae (14/23), Arctoteae (3/3) and Vernonieae (12/21). Both glandular and non glandular trichomes are divided into seven major types.

Presence of 'twin' or 'duplex' cypselar hairs is one of the characteristic features of the family Compositae and is prevalent in the tribes Cichorieae, Dicomeae, Pertyeae, Mutisieae and Vernonieae. This type of trichomes is less common in the tribes Arctoteae and Cardueae. Distribution and structure of trichomes have taxonomic significance at the generic and infrageneric level. However, their value

as taxonomic markers will be greatly increased when combined with other cypsela characters such as structure of carpopodium, stylopodium and pappus, as well as surface features of cypselar wall, etc. Certain taxa have unique types of trichomes regarded as apomorphies. Fusiform twin hairs have been noted in *Gerbera piloselloides*, whereas papillose twin hairs were noticed in *Actites megalocarpa*. Sometimes papillate hairs united to form a scale-like structure e.g. in *Crepis* and *Hypochaeris*. Multicellular non-glandular acroscopic hairs have been noticed in *Echinops sphaerocephalus*. In *Carlina*, glandular twin hairs were observed.

Keywords: Trichomes, twin hairs, mature cypselas, Compositae.

Introduction

The Compositae (Asteraceae) family is nested in the order Asterales of Campanulids according to the APG III classification (The Angiosperm Phylogeny Group 2009). The family has largest number of accepted species, ca. 24,000, among angiosperm plant families and is distributed throughout the globe except Antarctica (FUNK et al. 2009, FUNK 2010). The genera number 1600–1700. All available evidence indicates that the family is monophyletic (e. g., SMALL 1919, BREMER 1987, JANSEN & PALMER 1987, 1996, BREMER et al. 1992, HANSEN 1990, 1991a, b).

After the long outdated classifications of BENTHAM (1873 a, b) and HOFFMANN (1890), the new classification of the Compositae by BREMER (1994) was the first approach at a modern phylogenetic analysis of this family. BREMER's classification was morphologically based, but with subsequently rapidly developing molecular data a new picture of the family phylogeny emerged, first summarized by KADEREIT & JEFFREY (2007) and their associates. This modern approach culminated in the seminal and epoch-making work of FUNK et al. (2009). At present, the basal groups of Compositae are recognized as subfamilies like Barnadesioideae, Mutisioideae, Hyalideae, Wunderlichieae, Carduoideae, Pertyoideae and Cichorioideae. The present study includes some members of four basal subfamilies (Mutisioideae, Carduoideae, Pertyoideae and Cichorioideae).

Trichomes or hairs have long been of much importance in systematic investigation of angiosperms. Anatomically, a trichome or hair is an epidermal outgrowth of diverse form, structure and function (UPHOF 1962, ESAU 1965, FAHN 1986, 1988). Despite the great variety of systems proposed for the classification of trichome types, they are basically classified as either glandular with a secretory function or as covering hairs (non-glandular) without a secretory function (CUTTER 1978). Hairs originate from epidermal cells and develop on the outer surface of various plant organs (WERKER 2000). The hairs offer a rich field of investigation for a micro-morphologist because of their common occurrence and great diversity,

simplicity in structure and easy availability for observation due to their superficial position (SAHU 1982 a, b, c, 1983).

The types of hairs (epidermal outgrowths) have been reviewed and classified in early works, such as by DE BARY (1884) who recognized four major categories, viz., (i) Bladders, (ii) Hairs, (iii) Scales and (iv) Shaggy hairs. DE BARY (l.c.) also noted that the presence of hairs in plant organs is a universal character in vascular plants. Later COWAN (1950) merged the 'Shaggy hairs' into the category of 'hairs' and various other categorizations of trichome type have been put forward. Similar approaches have been made in various plant families. For example, GOEBEL (1900) was the first to discuss the significance and relationships of trichomes in the tribe Rhinanthae of the family Scrophulariaceae.

One pioneer in the study of role and importance of hairs in taxonomy and their phylogenetic evolution was SOLERADER (1908) in his work entitled "Systematic Anatomy of the Dicotyledons". He again divided the hairs into two major categories, viz. (i) the clothing hairs and (ii) the glandular hairs. SOLERADER (op.c.) described the hairs present on the ovary of *Spilanthes oleracea* (now *Acmella oleracea*) as follows: "they consist of two long hair cells which are jointed together lengthwise along one side, but diverse apically so as to resemble swallows tail." Such types of hair are characteristic of the ovary or cypsela (achene) in the family Compositae (RAMAYYA 1962 a, b, c) and these hairs were designated variously; e.g., 'Zwillingshaare' (KRAUS 1866, HESS 1938), translated to 'twin hairs' (e.g., VAUGHAN 1970, GRAU 1977, DITTRICH 1977), or 'biseriate forked hair' (NARAYANA 1979), simply 'achenial hair' (SMALL 1919, HESS 1938, RAMAYYA 1962 a, b, c, 1963, 1969, 1972, MANILAL 1963, SAHU 1976, 1978, 1979, 1980, 1982 a, b, 1983, 1984, FREIRE et al. 2002), or sometimes 'duplex hair' (e.g., MACLOSKIE 1883, NICHOLS 1893, NORDENSTAM 1977). Primarily a twin hair consists of two triangular or rectangular and usually short basal cells, completely or partly united with each other along their longitudinal walls (SANCHO & KATINAS 2002). NORDENSTAM (1968 b) described the twin hairs of *Euryops* as consisting of two parallel, short to elongate cells plus a smaller basal cell, i.e. three cells altogether.

Early records of the hairs of Compositae are usually brief and sometimes fragmentary, e.g. as reported by NICHOLS (1893), LLOYD (1901), KUPFER (1903), CAVILLIER (1907, 1911), HOLM (1908, 1913, 1917 & 1926), SABNIS (1921), BRIQUET (1916, 1930), DIETTERT (1938), ARTSCHWAGER (1943), VOLLE & HETZGER (1949) and MIRASHI (1955, 1956). Later more detailed accounts have been made such as the descriptions of glandular hairs of the subtribe Madinae presented by CARLQUIST (1958, 1959 a, b, c).

Another significant contribution regarding the hairs of Compositae has been documented by RAMAYYA (1962 a, b, c, 1963 & 1969). He described the structure,

variation and distribution of 35 types of hairs in some Compositae and their mode of development. He also recognized four distinct “Systems of hairs” in this family, viz., (i) Filiform Trichome System; (ii) Macroform Trichome System; (iii) M-Multiseriate Trichome System and (iv) P-Multiseriate Trichome System.

METCALFE & CHALK (1950, 1979, 1989) have stated that trichomes possess taxonomic value, that both glandular and non-glandular hairs are present in the Compositae, and that the non-glandular hairs are of various morphological types, whereas the glandular hairs are more or less homogeneous with a uniform structure.

Structures of hairs are greatly variable among different taxa. For example, SPRING (2000) has described more than 300 forms of plant trichomes.

Many workers have contributed on the systematic value of hairs in the genus *Vernonia* s.lat., like HUNTER & AUSTIN (1967) and FAUST & JONES (1973) in North American species, and NARAYANA (1979) on 15 South Indian species. In the latter 18 types of hairs were noted by NARAYANA (l.c.), out of which three types (biseriate vesicular glandular hair, biseriate non-forked hair and biseriate forked) were found on the ovary wall. Twenty Indian species of *Vernonia* were studied by SAHU (1984), who mentioned that the frequency distribution of cypselar (= achenial) hairs is highest (57%) among all the hairs observed. Five among the six cypselar hair types noted are of glandular type, viz. (i) biseriate glandular hair, (ii) biseriate vesicular glandular hair, (iii) biseriate capitate glandular hair, (iv) biseriate vesicular capitate glandular hair, and (v) multiseriate glandular hair, and one (vi) non-glandular hair type.

NORDENSTAM (1968b, 1977, 1978, 2006a, 2007) noted that the duplex hairs are widespread in the tribe Senecioneae but not in Calenduleae. He found that such hairs show various modifications and occasionally (e.g. in species of *Euryops*, *Mesogramma*, *Bolandia*, *Dauresia*, *Lomanthus*) exude mucilage when treated in water (NORDENSTAM & PELSER 2005, 2009). Similar type of duplex hairs has been observed by MACLOSKIE (1883), JAMES (1883), NICHOLS (1893), DRURY & WATSON (1965) and SAHU (1983), mainly in the Senecioneae, e.g. species of *Senecio*, *Othonna*, and *Euryops*. MACLOSKIE (1883) and SAHU (1976, 1978, 1979, 1980, 1982 a. b) also observed similar trichomes in other taxa of Compositae.

KING & ROBINSON (e.g., 1969, 1970, 1979) have used the hair structure along with other epidermal features in determining many generic circumscriptions in the Compositae, especially in the Eupatorieae.

In the systematic review of Cynareae, DITTRICH (1977) reported that cypselas in subtribe Echinopsinae (*Echinops* and *Acantholepis*) are densely covered by multicellular stiff hairs. In all members of the subtribe Carlininae, cypselas hairs

are 'twin hair' type. Members of the Cardueae have been studied in some detail by PETIT (1987, 1997).

NAPP-ZINN & EBLE (1980) studied the glandular and non glandular hairs of 20 genera of the Anthemideae. On the basis of differences of glandular hairs, three species of *Artemisia* are clearly separated, i.e., *A. nova*, *A. arbuscula* and *A. tridentata* (KELSEY & SHAFIZADEH 1980, KELSEY 1984).

The types of hairs may be considered as valuable accessory characters in plant taxonomy, particularly at infrageneric levels (STEBBINS 1953, FAUST & JONES 1973, NAPP-ZINN & EBLE 1980, SAHU 1978, 1979, 1980, 1982 a, b, 1984, HOOT 1991, KOROLYUK 1997).

SANCHO & KATINAS (2002) have shown the presence of typical twin type of hairs from the corollas of Mutisieae. In addition to that corollas also bear four other types of hairs. They have also indicated that the ontogenies of cypselar twin hairs and twin hairs of corollas were identical.

NORDENSTAM (1968a, 1978, 2006 b) and LUNDIN (2006) have pointed out that some members of the tribe Senecioneae possess more complex, stellate or substellate types of hairs, e.g., *Aequatorium* B. NORD. and *Nordenstamia* LUNDIN and rarely in *Euryops*, although not on the cypselas, which are glabrous (or glandular-puberulous). Substellate or T-shaped hairs occur also in *Dresslerothamnus* H. ROB. of the same tribe (ROBINSON 1989).

Microcharacters of glandular hairs from 34 species belonging to 7 tribes of the subfamily Asteroideae, have been studied by CICCARELLI et al. (2007) who discussed the usefulness of the glandular hairs of the ovary.

Leaves of the industrial oilseed *Vernonia galamensis* ssp. *galamensis* var. *ethiopica* GILBERT, contain glandular hairs, which are actually 10-celled peltate biseriate glandular hairs (cf. also below). Along with these hairs this taxon has awl-shaped glandular hairs and non-glandular hairs (FAVI et al. 2008).

The detailed structure of trichomes from stem and leaves of 135 species belonging to 53 genera in tribe Lactuceae was studied by KRAK & MRAZ (2008). They recognized eight types and several subtypes, and they have focused on the utility of hairs in the infratribal classification with the help of both light and scanning electron microscopy.

ANDREUCCI et al. (2008) studied critically the histochemistry and morphology of multicellular biseriate glandular hairs of *Matricaria chamomilla*. These hairs are composed of 10 cells, viz. two basal cells, two peduncle cells and a secretory head containing six cells. Ten-celled biseriate glandular hairs also have been reported by MONTEIRO et al. (2001) from the leaves of *Stevia rebaudiana* (tribe Eupatorieae).

Similar type of stalked glandular hair and two types of non-glandular hairs have been noted from the cypsela of *Stevia rebaudiana* by CORNARA et al. (2001).

ADEDEJI (2004) and ADEDEJI & JEWoola (2008) stated that hairs can be fruitfully used for the delimitation of genera within the family Compositae and they have mentioned different types of glandular and non-glandular hairs. The genus *Vernonia* can be delimited from other genera by the presence of T-shaped hairs and *Chromolaena* has amoeboid-shaped hairs.

Diversity of leaf hairs and phylogenetic relationships on the basis of such hairs in different taxa of *Artemisia* have been discussed by HAYAT et al. (2009a, b, c) using both light microscopy and scanning electron microscopy. Eight major types of hairs were distinguished in their study.

ROBINSON (2009) has correlated some hair characters with their chemical components. Glandular hairs may have different types of defensive components, viz. sesquiterpene lactones, monoterpenoids, gelatinous material with clerodane and labdane derivatives, which are usually common in Eupatorieae and Heliantheae. These two tribes are also characterized by the absence of T-shaped hairs. He has also emphasized the use of non-glandular hairs in different degrees. Hair characters support the separation of *Critoniopsis* SCH.BIP. from *Tephrothamnus* SCH.BIP. and *Eremosis* (DC.) GLEASON as proposed by KEELEY et al. (2007) on the basis of DNA studies.

Adding to the great variation in cypselar hairs, the tribe Gochnatieae (previously in Mutisieae) has three types of hairs, viz., two-armed, obliquely septate, and biseriate glandular (FREIRE et al. 2002). VENTOSA & HERRERA (2011 a, b) report the presence of biseriate glandular hairs with vesicle and simple biseriate non-glandular hairs on the cypselas of several species of *Anaethaphia* D. DON (formerly in genus *Gochmatia*).

The present study deals with the cypselas of 44 genera and 71 species of 7 tribes (Mutisieae, Dicomeae, Cardueae, Pertyeae, Cichorieae, Arctoteae and Vernonieae) under four subfamilies (Mutisioideae, Carduoideae, Pertyoideae and Cichorioideae). We thus briefly survey and summarize the variation of hairs from the mature cypselas belonging to the subfamily Cichorioideae sensu BREMER (1994), or the basal subfamilies and tribes sensu PANERO & FUNK (2002), FUNK et al. (2009) and FUNK (2010).

The objectives of this study are as follows:

- i) to elucidate the presence or absence of hairs on cypselar surface.
- ii) to present the types of hairs and location of hairs on the cypselar surface.
- iii) to describe the comparative morphological features of cypselar hairs in different genera and species.

- iv) to facilitate an accurate and rapid identification of taxa along with other cypselar features.
- v) to verify the potential usefulness of cypselar hairs for taxonomic or phylogenetic studies.
- vi) to investigate affinities among the analyzed taxa based on the distribution of hairs types.

Since micro-morphological features of hairs from different plant parts play such a significant role in plant taxonomy, particularly at the generic and specific levels, many plant anatomists and taxonomists have been attracted and fascinated by this subject and tried to prove the relationships of taxa on the basis of hair characters. Only a fraction of the rich literature has been summarized here. But knowledge about cypselar hairs and their taxonomic significance is still incomplete. Therefore, some additional information based on both light microscopy (LM) and scanning electron microscopy (SEM) is provided here.

Materials and Methods

This study is based on the mature cypselas from collections in AD, BRI, LISC, NSW, RB, SRGH, TAI and Z herbaria as designated in Index Herbariorum (HOLMGREN et al. 1990). Some cypselas were collected by the first author indicated as S. MUKHERJEE from some parts of India also and deposited in the Herbarium of the Department of Botany, University of Kalyani, Kalyani – 741235, India as indicated by the new herbarium acronym, KAL. A list of all studied taxa and their source of origin is given in Appendix I. Studied taxa were classified in tribes according to FUNK et al. (2009), with nomenclature updated to current knowledge (mostly according to the online version of THE INTERNATIONAL PLANT NAMES INDEX, Harvard University databases) and the genera and species are enumerated in alphabetical sequence.

For microscopic examination, mature dry cypselas were observed after boiling with water and fixed in FAA solution (JOHANSEN 1940). Some FAA preserved cypselas were boiled in saturated solution of chloral hydrate solution for 1–3 minutes and washed with water. Whole cypselas (both treated and untreated) were stained in 0.5% aqueous safranin solution and were mounted in 70% phenol glycerine solution for microscopic observation.

Camera lucida drawings were done using a compound trinocular research microscope. For each species, at least five randomly selected cypselas were examined.

For scanning electron microscopy (SEM) studies dry cleaned cypselas were placed directly on the stubs with double coated adhesive tape and coated with gold. The

cypselar surface with or without hairs was scanned and photographed in a Philips Electron Microscope at 15 KV in the Regional Sophisticated Instrumentation Centre of Bose Institute at Kolkata, West Bengal, India. A few SEM photographs were taken in Hitachi SEM at the University Scientific Instrumentation Centre (USIC) of the University of Burdwan, Burdwan, West Bengal, India.

Descriptive terminology for trichomes follows RAMAYYA (1962 a, b, c), NARAYANA (1979), PAYNE (1978) and CICCARELLI et al. (2007). However, simple self explanatory terms are included to identify the specific type of hair.

Discussion

Out of 71 studied species, 53 species (75%) have hairs on the mature cypselar surface and 18 species (25%) lack hairs. Of those possessing cypselar hairs, only six taxa (11%) possess only glandular hairs (G), 33 species (62%) have non-glandular hairs (NG), and remaining 14 species (26%) have both glandular and non-glandular hairs.

As indicated above the classification of Compositae has been recently thoroughly revised, but is still in some groups in a state of flux. BREMER (1994) in his cladistic classification of Compositae mentioned that in spite of the beginning accumulation of modern molecular data, a continued detailed study of morphological characters is necessary for the construction of robust phylogenies. This statement is still valid today.

Detailed morpho-anatomical studies of cypselas have been performed at least since the time of SCHULZ-BIPONTINUS (1844 a, b), and important pioneering work by BERKHEY (1761). GAERTNER (1790) and numerous contributions by HENRI CASSINI (1781 – 1832) must also be acknowledged. In later times, many workers (e.g., BRIQUET 1916, 1930, BLAKE 1918, GIROUX 1930, KYNČLOVÁ 1970, GRAU 1977, 1980, SAENZ 1981, VALEZ 1981, PANDEY et al. 1982, MUKHERJEE 2000, 2001 a, b, 2008, DAS & MUKHERJEE 2008) have clearly indicated that diacritical features of cypselas could be used for the delimitation, characterization and phylogenetic relationships among the taxa of Compositae. Important features of cypselas include general morphology, presence or absence of ribs, carpopodium, stylopodium, pappus, surface trichomes, phytomelanin layer, calcium oxalate crystals, and tissue organization of pericarp and testa. All these characters are genetically controlled (LANE 1985, CRAWFORD et al. 2001). These micro-characters of cypselas are used for characterization of taxa at the generic and specific level and also for improvement of existing system of classification. (cf. KÄLLERSJÖ 1985, MUKHERJEE 2000, 2001 a, b, MUKHERJEE & SARKAR 2001a,b,c, MUKHERJEE & NORDENSTAM 2004, 2008, 2010). Therefore, cypselar hairs are part of the set of

microcharacters which all play similar roles along with other features.

Basic structure, distribution and apical part of hairs are all significant at the specific level. Morphological similarity in such details often reflects taxonomic closeness as pointed out by ANDERBERG (1989, 1991 a, b) and ELDENÄS et al. (1996). An example from the present study is provided by *Crepis* and *Hypochaeris* which have identical types of hairs. Both genera belong to the tribe Cichorieae and they are related (Clade 4 in KILIAN et al. 2009).

HESS (1938) has argued that the principal function of 'twin hairs' is absorption of water, particularly those which have thickened walls. According to him, this type of hairs has sufficient amount of pits which facilitate the absorption of humidity from surrounding atmosphere. Therefore plants with such type of cypsalar hair can thrive in arid and semiarid regions. Myxogenic 'twin hairs' keep the moisture around the cypselas as a mucilaginous layer, thus facilitating germination and/or perhaps contribute to seed dispersal. Present study indicates that phylogenetically widely separated tribes (e.g., Mutisieae and Cichorieae) possess twin type of hairs, which are also recorded in literature from many different groups of the family. So, this phenomenon may represent a convergent evolution in different tribes in response to similar environmental conditions.

Secretory substances within the glandular hairs are thought to protect plants against herbivores and pathogens, and at the same time they might reduce the loss of water through cuticular transpiration as well as maintaining the temperature of the leaves (DELL & MCCOMB 1975, 1977, KELSEY & SHAFIZADEH 1980, WERKER & FAHN 1981, DUKE et al. 1994, TATTINI et al. 2000). Glandular trichomes of *Stevia rebaudiana* contain sesquiterpene lactones, which are widespread throughout the family in various organs. Presence of such compounds, which have a bitter taste and may be toxic to grazing animals, should be of importance in the protection of plants against herbivores.

According to MAYEKISO et al. (2008), the non-glandular trichomes "appeared to originate from the epidermal layer by periclinal division. This process continued by periclinal division until several cells which formed the uniseriate trichomes, was produced".

Hairs are directly attached to, or in close contact with the surrounding environment, so their role must be largely protection from adverse biological, chemical and physical conditions. Absorbing and secretory activity of hairs also influence pollination and seed dispersal (cf. above, and UPHOF 1962, WERKER 2000).

Presence of 'twin hairs' indicates that the studied subfamilies (Mutisioideae, Carduoideae, Pertyoideae, Cichorioideae) are apomorphic in relation to the primitive subfamily Barnadesioideae, characterized by its 'barnadesioid hairs'

(CABRERA 1959, 1977, BREMER 1987, BREMER & JANSSEN 1992, KATINAS & STUESSY 1997, GRUENSTAEUDL et al. 2009). These are generally three-celled trichomes often with a long apical cell, a basal isodiametric cell, and an attached epidermal cell (two parallel cells).

Variation of 'twin hair' structure was indicated already by HESS (1938) and further discussed by FREIRE & KATINAS (1995). Present study also shows the variation of twin hairs in different taxa.

Biseriate (usually 10-celled) glandular hairs are common in Compositae (CARLQUIST 1958, 1959a, b, c, 1961), but not observed in mature cypselas. Such hairs have been reported from various tribes of several subfamilies, e.g. Mutisieae (CASTRO et al. 1997); Vernonieae (NARAYANA 1979, CASTRO et al. 1997) and Cardueae (SCHNEPF 1969). Peltate glands are very prominent in different species of *Vernonia*. These are visible with simple dissecting microscope. Such glandular hairs were termed as 'bilobed hairs' by FAUST & JONES (1973), and they are apparently common in the tribe Vernonieae.

Our study also confirmed that mature cypselar hairs of Compositae are often good taxonomic markers and can be utilized to resolve the taxonomic affinity of a group. For example, the tribe Vernonieae is mainly characterized by the presence of both glandular and non-glandular hairs in many studied genera, e.g. *Centrapalis*, *Lepidaploa*, *Polydora*, *Vanillosmopsis*, *Vernonanthura* and *Vernonia*. Previously almost all these taxa have been included in the genus *Vernonia* (e.g., JONES 1977).

CICCARELLI et al. (2007) discussed the distribution of hairs on the ovary surface in different taxa of Compositae. The distribution of hairs is perhaps remaining constant within a species. Shape of the hair tip is greatly variable and sometimes species specific according to the documentation by CICCARELLI et al. (l.c.). Our findings agree with these observations.

Examination with the SEM revealed the presence of two types of hairs, corresponding to the two general types recognized in many previous works (cf. above). The non-secreting or non-glandular type is abundant and responsible for covering or protecting the cypselar surface. Secreting hairs are usually club-shaped or spheroidal glandular structures of varying size and shape. The cuticular striations are either smooth or reticulate in nature. On the basis of this character two species of *Cicerbita* (*C. cyanea* and *C. macrorhiza*) can be easily distinguished.

NARAYANA (1979) has reported three types of trichomes from the cypselas of *Vernonia*. He designated the 'twin hair' as 'biseriate forked hair'. His other two types of hairs have not been observed in the present study. Out of six hair types from 20 species of *Vernonia* reported by SAHU (1984), only the 'twin hair' was observed in the present study (by SAHU designated as "achenial hair"). The peltate

gland is usually found mainly on the leaves of *Vernonia* spp. This type of gland was designated as 'bilobed trichome' by FAUST & JONES (1973), and also found on the mature cypselas of different taxa of Vernonieae. Actually this gland is composed of 10 cells (cf. above). Such type of trichome has been noted by FAVI et al. (2008) from *Vernonia galamensis* ssp. *galamensis* var. *ethiopica*.

In *Arctotheca*, the entire cypselas is completely embedded in white indumentum formed by filiform, entangled hairs with simple obtuse apex but not 'twin' type, while in *Arctotis*, the major portion of cypselar surface is glabrous, except near the base, where it possesses numerous, white, 3–5.5 mm long 'twin hairs', whereas in *Berkheya* the entire cypselar surface bears 'twin hairs' of varying size. On the basis of these hair characters these three genera of Arctoteae can be easily distinguished.

According to BREMER (1994) and earlier system of classifications (BENTHAM 1873a,b, CABRERA 1977) *Ainsliaea*, *Gerbera* and *Dicoma* belonged to the tribe Mutisieae. But on the basis of recent studies (PANERO & FUNK 2002, KADEREIT & JEFFREY 2007, FUNK et al. 2009) these three genera have been included in three distinct tribes. *Gerbera* remains in Mutisieae (subfamily Mutisioideae), whereas *Dicoma* (and *Macledium* CASS. now recognized as separate) belong in the tribe Dicomeae of the subfamily Carduoideae and *Ainsliaea* in the tribe Pertyeae under the subfamily Pertyoideae. If we look into structure of hairs on cypselas, these three taxa each have a distinct type of hairs as well as a distinct type of cypselar tissue organization (MUKHERJEE 2001a). These findings support the separation of these and related taxa into three different tribes.

In Cardueae, cypselar surface is often bossed, seldom cross rugose (*Arctium*), covered by unicellular hairs (*Centaurea cyanus*), possessing scabrous multicellular hairs (*Echinops*) or carrying 'twin hairs' (*Carlina*) or glabrous in others. Majority of aforesaid types except unicellular hairs have been mentioned by DITTRICH (1977) from this tribe. The unicellular hair on the cypselar surface of *Centaurea* has been reported by BRIQUET (1930), however. A small swollen and glandular hair-like outgrowth is seen at the base of each side of the cypselas in *Cirsium japonicum*. Such type of hair has not been found in other studied species of this tribe. PETIT (1997) has used cypselar trichomes along with other morphological characters to elucidate relationships in Cardueae.

In mature cypselas, variation of hairs is significantly less than in the young cypselas or in the vegetative organs. Only seven basic types of hairs have been observed in the present study, whereas numerous and various types of trichomes have been noted by different workers either from the vegetative part or from the young reproductive parts in other taxa. The basic types of hairs observed by us are as follows:

1. Twin hairs; 2. Papillate hairs; 3. Vesicle-like capitate glandular hairs;
4. Non-glandular filiform hairs; 5. Multicellular non-glandular acroscopic hairs;
6. Simple hairs; 7. Unicellular hairs.

Among these the twin hairs, papillate types and vesicle-like capitate glandular hairs are predominant. This is perhaps due to their persistent nature as compared to the deciduous nature of other types of hairs. Similarly detailed cellular configuration of hairs is not clearly visible in mature state of the cypselas. Therefore the detailed cellular structure of hairs has not been included here.

1. Twin type of hairs

These are prevalent in studied tribes Dicomeae, Pertyeae, Mutisieae, Cichorieae and Vernonieae, but less common in the tribes Arctoteae and Cardueae. Twin hairs again can be broadly categorized on the basis of shape of the terminal and basal cells into the following subtypes:

- i) Long twin hairs : consisting of long laterally adpressed cells: *Ainsliaea latifolia*, *A. reflexa*, *Berkheya zeyheri*, *Carlina vulgaris*, *Catananche caerulea*, *Macleodium sessiliflorum*, *Vernonanthura diffusa*, *Vernonia scorpioides*,
- ii) Short twin hairs : arm or apical cells are short in length: *Gerbera jamesonii*, *Vernonia glabra*.
- iii) Apical ends of the arm or apical cells at distinctly unequal levels: *Ainsliaea latifolia*, *Baccharoides calvoana* ssp. *meridionalis*, *Vernonanthura diffusa*, *Vernonia cistifolia*.
- iv) Apical ends of the arm or apical cells more or less in equal plane: *Catananche caerulea*, *Elephantopus scaber*, *Lepidaploa gracilis*, *Polydora bainesii*, *Polydora poskeana*, *Vernonia glabra*, *Vernonia scorpioides*.
- v) Free portion of arm cells or apical cells greater in length than the basal united portion: *Baccharoides anthelmintica*, *Centrapalis kirkii*.
- vi) Papillate twin hairs: two papilla-like cells united to form twin hair: *Cicerbita cyanea* (only found in ribs region).
- vii) Fusiform twin hairs: arm cell thin-walled, more or less equal in length with abruptly attenuated tips, usually coloured (pink): *Piloselloides hirsuta*.
- viii) Base of twin hairs bilobed: *Gerbera jamesonii*.
- ix) Basal cells of twin hairs distinctly recurved: *Macleodium sessiliflorum*.

On the basis of orientation or distribution of twin hairs on the cypselar surface,

hairs may be following types.

- i) Densely distributed throughout the cypselar surface, e.g., *Carlina acanthifolia*, *Vernonia cistifolia*, *Vernonia glabra*, *Vernonia scorpioides*.
- ii) Sparsely distributed throughout the cypselar surface, e.g., *Lepidaploa gracilis*.
- iii) Restricted (mainly) to furrow region, e.g., *Linzia melleri*.
- iv) Restricted (mainly) to ribs region, e.g., *Polydora bainesii*, *Vernonia petersii*.
- v) Mainly concentrated towards the lower part of cypselar surface, e.g., *Gerbera jamesonii*.
- vi) Mainly concentrated towards the apical part of cypselar surface, e.g., *Cicerbita macrorrhiza*.

2. Papillate hairs

Papillate hairs are usually present in the majority of studied taxa of the tribe Cichorieae. On the basis of structure of other types of hairs and distribution of papillate hairs on the cypselar surface, the members of Cichorieae can be grouped into the following types:

- i) Papillate hairs moderately long with granule-like micro-projections as secondary sculpture, e.g., *Cicerbita cyanea*, *Lactuca serriola*.
- ii) Papillate hairs without micro-projections, e.g., *Actites megalocarpa*, *Cicerbita macrorrhiza*, *Taraxacum officinale*.
- iii) Papillate hairs extremely minute and randomly dispersed, e.g., *Hieracium villosum*.
- iv) Numerous minute papillate hairs arranged in several transverse rows and forming a transversely muricate surface, e.g., *Scorzoneroide autumnalis*.
- v) Papillate hairs free at the furrows, but on the ribs papillate hairs laterally connate with each other and forming multicellular scale-like structures. Based on the shape of these scale-like structures there are three subtypes:
 - a) Apex of the scale nearly flat, e.g., *Crepis vesicaria*.
 - b) Apex of the scale nearly triangular, e.g., *Hypochaeris glabra*.
 - c) Apex of the scale nearly rounded, e.g., *Hypochaeris radicata*.
- vi) Papillate hairs with wide bifurcate base and pointed apex, e.g., *Taraxacum officinale*.

- vii) True papillate hairs absent, but surface squamosely muricate. Muricae vertically elongated with rounded broad elevation. Epidermal cells form obscurely papilla-like structures with obtuse apex, e.g., *Tragopogon porrifolius*.
- viii) Cypselar surface with papillate hairs at the furrows and moderately long papillate twin hairs on the ribs, e.g., *Actites megalocarpa*, *Cicerbita cyanea*.
- ix) Cypselar surface without papillate hairs but with long twin hairs, e.g., *Catananche caerulea*.
- x) Cypselar surface without any type of hairs but cross rugose or cross marked, e.g., *Sonchus brachyotms*.

3. Vesicle-like capitate glandular hairs

These are prevalent in the tribe Vernonieae. On the basis of distribution and structure of these hairs on the cypselar surface the following categories are recognized:

- i) Glandular hairs uniformly distributed throughout the cypselar surface, e.g., *Vernonia colorata*.
- ii) Glandular hairs sparsely distributed on the furrows only, and cypselar hairs may be of two types:
 - a) Glandular hairs homomorphic, e.g., *Centrapalis kirkii*, *Gymnanthemum amygdalinum*, *Lepidaploa gracilis*, *Polydora bainesii*, *Vanillosmopsis capitata*, *Vernonanthura diffusa*, *Vernonia cistifolia*, *Vernonia petersii*, *Vernonia scorpioides*. In *Polydora bainesii* each glandular hair has three distinct zones and in *Polydora poskeana* each glandular hair has two semi-lunar hyaline spaces at the two opposite sides (visible after clearing).
 - b) Glandular hairs dimorphic, e.g., *Rolandra fruticosa*, *Vernonia colorata*.
- iii) Glandular hairs densely distributed on the furrows of cypsela. There are three subcategories:
 - a) Glandular hairs arranged in 4–9 vertical zones, e.g., *Bothriocline laxa*, *Centrapalis kirkii*, *Polydora bainesii*, *Vernonia cistifolia*.
 - b) Glandular hairs arranged in 1–3 vertical rows, e.g., *Gymnanthemum amygdalinum*, *Lepidaploa gracilis*, *Vanillosmopsis capitata*, *Vernonanthura diffusa*.
 - c) Glandular hairs arranged in 1–2 vertical rows in two sides of each furrow, e.g., *Baccharoides calvoana*, *Linzia melleri*, *Vernonia glabra*.

4. **Multicellular non-glandular acroscopic hairs.** This type is found in only one species, viz., *Echinops sphaerocephalus*.
5. **Unicellular hairs.** This unbranched non-glandular hair type was observed in *Centaurea cyanus* and *Cirsium vulgare*.
6. **Simple hairs**, i.e. unbranched multicellular non-glandular hair type, e.g., *Arctotheca calendula*, *Arctotis venusta*, *Centrapalis kirkii*, *Lactuca serriola*, *Tragopogon porrifolius*.
7. **Non-glandular filiform hairs.** These hairs have a basal bulbous portion and a long filiform terminal part, e.g., *Linzia melleri*.

Conclusion

From the above discussion it is obvious that micro-morphological characters of hairs along with other microcharacters of cypsela or other vegetative or floral morphological characters can be used for taxonomic and phylogenetic studies in the Compositae. There is a need to develop better universal terminology and perform detailed comparative studies of these micro-morphological features to improve Compositae taxonomy. An intensive morphological and ultrastructural study of cypsela hairs of cypsela along with other features of cypsela will make it possible to identify species in the fruiting state even when plants in flower are not available.

The present study also suggests that the value of hairs as a taxonomic criterion will be greatly increased when combined with other lines of evidence.

Table 1. Types and distribution of hairs in mature cypselas of Compositae in the present study.

SSL no. (1)	Taxa (2)	Presence (+) or absence (-) of hairs (3)	Types of hairs: glandular (G) or non glandular (NG) hairs (4)	Morphological nature of hairs on the mature cypselar surface (5)
	Tribe Mutisieae			
1)	<i>Gerbera jamesonii</i> (Figs. 1, 2)	+	NG	Cypselar surface sparsely covered by thin-walled short stiff persistent twin hairs more or less identical in structure. Base of the twin hairs bilobed. Tips of hair cells situated more or less on same plane.
2)	<i>Leibnitzia nepalensis</i>	+	NG	Structure and distribution of hairs more or less identical with the previous one.
3)	<i>Piloselloides hirsuta</i> (Fig. 3)	+	NG	Short fusiform thin-walled pink coloured twin hairs densely distributed throughout the surface. Tips of the twin cells abruptly attenuate and situated in equal plane.
	Tribe Dicomeae			
4)	<i>Macledium sessiliflorum</i> ssp. <i>sessiliflorum</i> (Figs. 4, 5, 6, 108)	+	G	Cypselar surface densely covered by slender stiff white about 1.0 – 1.5 mm long twin hairs. Length of the hairs variable. Basal cells of the glandular hairs much wider than the base of the body cells of the hair and basal glandular cells contain brown coloured substances. Basal portion of hairs often recurved. Hairs also observed in SEM photographs.

	Tribe Cardueae				
5)	<i>Arctium lappa</i> (Figs. 7, 88)	-			Cypselar surface glabrous, i.e. without hairs, but cross rugose by numerous black patches throughout.
6)	<i>Carduus defloratus</i>	-			Cypselar surface somewhat bossed and finely striated and glabrous.
7)	<i>Carlina acanthifolia</i> ssp. <i>cynara</i> (Figs. 8, 9, 96)	+		G	Cypselar surface densely covered by acroscopic stiff light yellow to light brown long shortly forked twin hairs. Foot cell of each glandular hair deep brown in colour.
8)	<i>Carlina vulgaris</i> ssp. <i>vulgaris</i> (Figs. 10, 11)	+		G	Same as preceding.
9)	<i>Centaurea cyanus</i> (Figs. 12, 13, 97, 98)	+		NG	Cypselar surface sparsely covered by soft short fine pale yellow unicellular shiny hairs.
10)	<i>Centaurea macrocephala</i>	-			Cypselar surface glaucous glabrous.
11)	<i>Centaurea maculosa</i>	-			Same as preceding.
12)	<i>Cirsium arvense</i>	-			Cypselar surface glaucous glabrous.
13)	<i>Cirsium falconeri</i>	-			Cypselar surface glaucous like in <i>C. arvense</i> .
14)	<i>Cirsium japonicum</i> (Fig. 14)	+		G	Cypselar surface somewhat bossed without twin hairs, but two sides near the base bear two glandular hair like outgrowths.
15)	<i>Cirsium vulgare</i> (Fig. 15)	-			Cypselar surface somewhat bossed with numerous vertically elongated discrete black patches.

16)	<i>Echinops sphacrocephalus</i> (Figs. 16, 17, 101)	+	NG	Cypselar surface densely covered by multicellular, acroscopic hairs with sharply pointed apex.
17)	<i>Ptilostemon diacantha</i>	-	-	Cypselar surface glabrous, but with many large blackish brown somewhat bossed patches.
18)	<i>Rhaponticum scariosum</i> ssp. <i>rhaponticum</i>	-	-	Cypselar surface glabrous.
19)	<i>Saussurea abnormis</i>	-	-	Cypselar surface glabrous.
20)	<i>Saussurea deltoidea</i> (Fig. 18)	-	-	Cypsela surface with scale-like projections but without hairs.
21)	<i>Saussurea heteromalla</i>	-	-	Cypsela surface having cross rugosity with fringed margins.
	Tribe Pertyeae			
22)	<i>Ainsliaea aptera</i>	+	NG	Cypsela surface sparsely covered by soft short silky thin-walled dark coffee-coloured twin hairs with equally sized arms.
23)	<i>Ainsliaea latifolia</i> (Figs. 19, 20, 36)	+	NG	Cypsela surface very densely covered by slender stiff persistent acroscopic twin hairs. Basal cell of twin hairs more or less same in diameter throughout the length of the hair. Tips of the apical cells of the hair situated in prominently distant planes.
24)	<i>Ainsliaea reflexa</i> var. <i>ninborum</i> (Fig. 87)	+	NG	Twin hairs densely distributed on the entire cypselar surface except carpodial region. Twin hairs more or less same as preceding.
	Tribe Cichorieae			

25)	<i>Actites megalocarpa</i> (Figs. 21, 85)	+	NG	Cypselar surface minutely papillate throughout except at the top of the ribs region, where papillate twin hairs are present. Cypselar surface not cross rugose.
26)	<i>Catananche caerulea</i> (Fig. 22)	+	NG	Cypselar surface sparsely covered by long persistent twin hairs with more or less equal tips.
27)	<i>Cicerbita cyanea</i> (Fig. 23)	+	NG	Cypselar surface densely covered by numerous short papillate hairs with sharply pointed apex. Papillate type of twin hairs found in the ribs region.
28)	<i>Cicerbita macrorhiza</i> (Figs. 24, 25, 26, 27, 28, 99)	+	NG	Cypselar surface densely covered by numerous short papillate hairs with blunt ends. Surface with two types of twin hairs: one with distinctly unequal tips, other with more or less equal blunt tips. In addition papillate twin hairs and long unicellular hairs also present - altogether five types of hairs present on cypselar surface.
29)	<i>Crepis pyrenaica</i>	-	-	Cypselar surface glabrous.
30)	<i>Crepis vesicaria</i> (Figs. 29, 100)	+	NG	Cypselar surface densely covered by two types of hairs. At the ribs, papillate hairs laterally connate with each other forming a multicellular (4-9 cells) scale-like structure almost flat at the apex; whereas papillate hairs are discrete and free at the furrows. Entire cypselar surface or hair surface with numerous micro-projections.
31)	<i>Hieracium villosum</i> (Figs. 30, 102)	+	NG	Entire cypselar surface with conspicuously small acroscopic randomly distributed papillate hairs.
32)	<i>Hypochaeris glabra</i> (Figs. 31, 103)	+	NG	Cypselar surface more or less identical with <i>Crepis vesicaria</i> except at the apical part of multicellular scale-like structure nearly triangular in shape. Secondary sculpture of hairs and surface somewhat micro-warty.

33)	<i>Hypochaeris radicata</i> (Figs. 32, 33, 104)	+	NG	Cypselar surface nearly similar to <i>Crepis vesicaria</i> except the apical part of the multicellular scale-like structure more or less rounded. Secondary sculpture micro-warty like <i>C. vesicaria</i> and <i>Hypochaeris glabra</i> .
34)	<i>Lactuca dissecta</i>	+	NG	Cypselar surface densely covered by minute papillate hairs evenly distributed.
35)	<i>Lactuca graciliflora</i>	+	NG	Cypselar surface densely covered by light brown to dirty white papillate evenly distributed hairs.
36)	<i>Lactuca serriola</i> (Figs. 34, 105)	+	NG	Cypselar surface densely covered by numerous moderately long papillate hairs with acuminate apex. Hairs more conspicuous near the apical part of cypselar. Cypselar surface including hairs possess granule-like micro-projections.
37)	<i>Launaea acutis</i>	-	-	Cypselar surface glabrous.
38)	<i>Launaea asplenifolia</i>	-	-	Cypselar surface glabrous.
39)	<i>Launaea procumbens</i>	-	-	Cypselar surface glabrous.
40)	<i>Launaea sarmentosa</i>	-	-	Cypselar surface glabrous.
41)	<i>Scorzonoides autumnalis</i> (Figs. 35, 106)	+	NG	Cypselar surface with numerous short triangular papillate hairs arranged in different vertical planes and surface appears as transversely muricate. Apical part of each papilla possesses pigmented substances.

42)	<i>Picris hieracioides</i>	+	NG	Cypselar surface transversely rugose with free papillate hairs on the furrows and papillate twin hairs on the ribs.
43)	<i>Prenanthes khasiana</i>	+	NG	Cypselar surface minutely papillate throughout and with papillate twin hairs on the ribs only.
44)	<i>Sonchus brachyotus</i> (Fig. 113)	-	-	Cypselar surface glabrous and finely cross rugose or cross marked at the ribs.
45)	<i>Sonchus schweinfurthii</i>	+	NG	Cypselar surface with numerous randomly distributed minute papillate hairs having pigmented substances inside. Cypselar surface not cross rugose.
46)	<i>Taraxacum officinale</i> (Fig. 36)	+	NG	Cypselar surface densely covered by numerous papillate hairs with obtuse apex and bifurcate base.
47)	<i>Tragopogon porrifolius</i> (Figs. 37, 114)	+	NG	Major portion of cypselar surface squamosely muricate at the ribs (not papillate or hairy). Murica vertically elongated with rounded broad elevation. Apical part of cypselar adjacent to pappus with numerous long filiform simple hairs.
	Tribe Arctoteae			
48)	<i>Arctolitea calendula</i> (Figs. 38, 89)	+	NG	Entire cypselar densely and completely covered by numerous persistent very fine and slender white filiform woolly hairs with single obtuse apex. Basal end of cypselar with tail-like similar tufted long hairs.
49)	<i>Arctotis venusta</i> (Figs. 39, 90)	+	NG	Cypselar surface glabrous except at the basal end, which bears numerous silky very fine white 3.5 – 5 mm long tufted hairs with rounded apex, but not twin type.

50)	<i>Berkheya zeyheri</i> ssp. <i>zeyheri</i> (Figs. 40, 93)	+	NG	Cypselar surface sparsely to densely covered by numerous fine short to long variable thin-walled persistent twin hairs with apical ends in equal plane.
	Tribe Vernoniae			
51)	<i>Baccharoides anthelmintica</i> (Figs. 41, 91)	+	G + NG	Cypselar surface with capitate glandular hairs sessile ellipsoid vesicle-like arranged in 1–2 rows in each furrow region, and upwardly directed 'twin hairs' present throughout the surface with more or less equal apical cells. Outer surface of the vesicle-like capitate glandular hairs smooth without reticulate cuticular striations.
52)	<i>Baccharoides calvoana</i> ssp. <i>meridionalis</i> (Figs. 42, 43, 92)	+	NG	Ridges of cypselar surface densely covered by long chocolate brown persistent twin hairs with nearly equal tips. Hairs more conspicuous towards the base of cypselar.
53)	<i>Bothriocline laxa</i> (Figs. 44, 45, 94, 95)	+	G	Hairs sessile capitate ellipsoid vesicle-like arranged in 4–9 vertical rows in each furrow from the base to apex. These are thick-walled, filled with secretory substances. Hairs pentangular to hexangular in outline in SEM with reticulate cuticular striations.
54)	<i>Centropetalis kirkii</i> (Figs. 46, 47, 48)	+	G + NG	Cypselar surface sparsely covered by many long very narrow thin-walled twin hairs. Free portion of terminal cells of the twin hair always longer than the basal united portion. Also large number of free heteromorphic vesicle-like capitate glandular hairs irregularly arranged on the furrows.
55)	<i>Elephantopus scaber</i> (Fig. 49)	+	G + NG	Glandular hairs vesicle-like thick-walled capitate sessile obovoid to ellipsoid, found in furrows, distributed sparsely. Twin hairs sparsely distributed in the furrows with more or less equal cells.

56)	<i>Gynnanthemum amygdalinum</i> (Figs. 66, 67)	+	G + NG	More or less identical with <i>Polydora bainesii</i> , but tip cells situated in distinctly unequal level. Capitate sessile glandular hairs free not coalesced with each other.
57)	<i>Lepidaploa gracilis</i> (Figs. 50, 51, 52)	+	G + NG	Furrow region of cypselar surface densely covered by acroscopic long thin-walled persistent twin hairs with more or less equal terminal ends. Many circular to elliptic vesicle-like capitate glandular hairs usually coalesced, sometimes free, distributed in furrows.
58)	<i>Linzia melleri</i> (Figs. 53, 54, 55, 107)	+	G + NG	Furrow regions of cypselar surface possess both twin hairs and capitate vesicle-like glandular hairs. Glandular hairs arranged uniseriately, occasionally biseriately in each side of furrow. Seldom 2-celled glandular filiform hairs present at the apical part of cypselar.
59)	<i>Polydora bainesii</i> (Figs. 56, 57, 58, 109, 110)	+	G + NG	Sessile capitate vesicular glandular hairs irregularly arranged in the furrow region, free or coalesced. Each glandular hair differentiated into 3 distinct zones: outer transparent, middle compact, and inner semitransparent zone. Twin hairs long, distributed throughout the surface but more numerous near ribs. In SEM, glandular trichome obovoid, with smooth surface, with terminal tubercle like short outgrowth.
60)	<i>Polydora poskeana</i> (Figs. 59, 60, 61)	+	G + NG	Ribs 3--5 times narrower than furrows and densely covered by thick-walled persistent twin hairs with more or less equal terminal cells. Furrows possess numerous ellipsoid to globose free large oriented capitate glandular hairs. Each glandular hair characterized by the presence of 2 semi-lunar hyaline spaces at the two opposite sides (after clearing).

61)	<i>Pseudolephantopus spicatus</i>	+	NG	Basal portion of cypselar surface and ribs region densely covered by long narrow thin-walled twin hairs with more or less equal tips.
62)	<i>Rolandra fruticosa</i> (Figs. 62, 63, 111, 112)	+	G	Hairs sessile thick-walled bilobed subglobose sparsely distributed throughout the surface. In SEM these appear homomorphic napiform bilobed and conspicuously depressed or notched at the middle with smooth cuticular striations. After clearing surface shows dimorphic glandular hair-like structure in 3–8 vertical rows.
63)	<i>Vanillosmopsis capitata</i> (Figs. 64, 65, 115)	+	G	Hairs sessile ellipsoid thick-walled, free in pairs and arranged in 2–3 vertical rows, found in furrow regions only, containing yellow substances.
64)	<i>Vernonanthura diffusa</i> (Figs. 68, 69, 70)	+	G + NG	Similar to <i>Gynnanthemum amygdalinum</i> but vesicle-like capitate glandular hairs arranged in groups or singly in 1–4 vertical rows. Twin hairs with distinctly unequal tips.
65)	<i>Vernonia cinerea</i>	+	G + NG	Cypselar surface sparsely covered by moderately long thin-walled twin hairs with slightly unequal tips. Furrow region possesses many vesicle-like ovoid glandular hairs, usually arranged in 1–3 vertical rows.
66)	<i>Vernonia cistifolia</i> (Figs. 71, 72, 73, 116)	+	G + NG	Capitate glandular hairs free sessile ellipsoid to circular from the top view and triangular from side view, distributed randomly on the furrows. Twin hairs short, distributed throughout the surface but more concentrated near ribs. In SEM glandular trichome with rounded apex and one deep wide circular depression at the centre, with smooth surface.

67)	<i>Tarlinomia elliptica</i>	+	G	Twin hairs not found on the cypselar surface, but multicellular vesicle-like glandular hairs found on the furrow regions arranged in 3–4 vertical rows.
68)	<i>Vernonia colorata</i> ssp. <i>colorata</i> (Figs. 82, 83, 84, 120)	+	G	Ribs usually wider than furrows and covered by numerous coalesced very small globose thick-walled glandular hairs. Furrow regions with free large ellipsoid to subglobose and unevenly distributed vesicle-like glandular hairs. Twin hairs absent. Capitate glandular hairs distinctly dimorphic.
69)	<i>Vernonia glabra</i> (Figs. 74, 75, 76, 117)	+	G + NG	Both ribs and furrow region of the cypselar surface covered by short twin hairs. Capitate vesicle-like glandular hairs arranged in 1 or 2 vertical rows on both sides of the furrow and coalesced with each other and each hair has a large central cavity.
70)	<i>Vernonia petersii</i> (Figs. 77, 78, 118)	+	G + NG	Ribs 2–3 times narrower than furrows. Cypselar surface densely covered by long stiff twin hairs in many rows with more or less equal tips. Capitate vesicle-like glandular hairs arranged in 1–3 rows in transverse plane to form horizontal strip-like structure. Glands usually coalesced with each other.
71)	<i>Vernonia scorptoides</i> (Figs. 79, 80, 88, 119)	+	G + NG	Cypselar surface, especially furrow regions, covered by slender long persistent twin hairs with slightly unequal tips. Furrows region possesses capitate vesicle-like glandular hairs in many rows, usually coalesced.

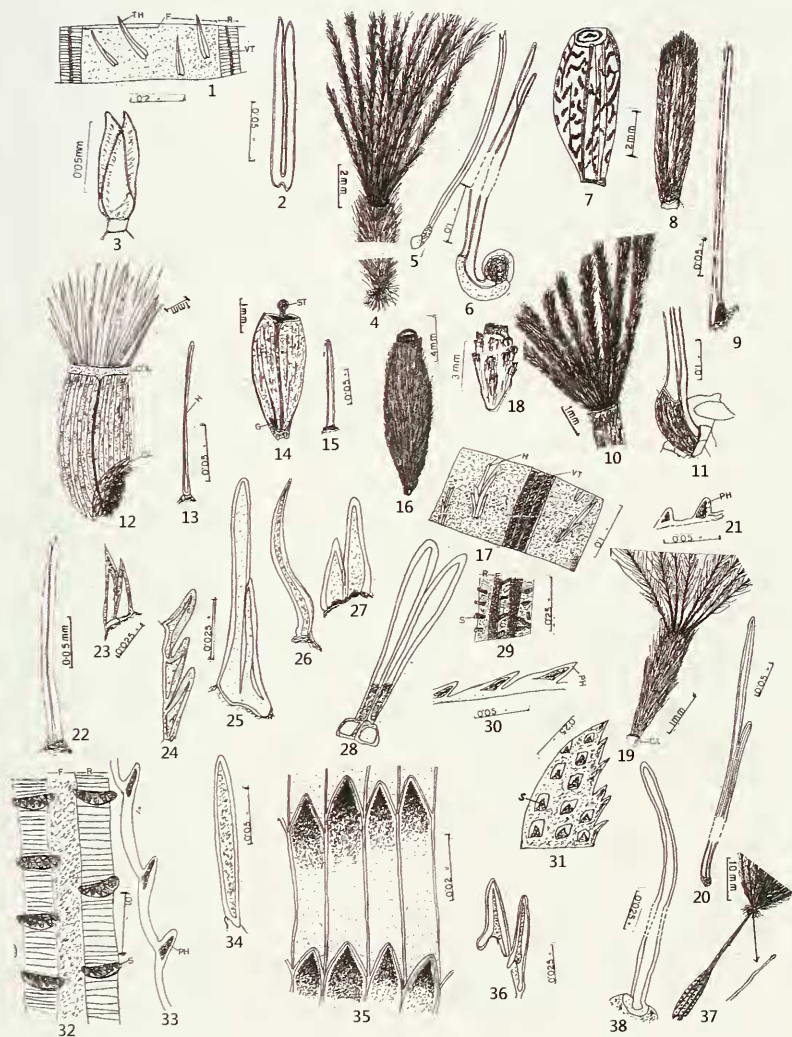
Appendix 1. Taxa studied and specimen location.

Sl. No.	Name of the Species	Tribe	Source of Origin
1.	<i>Actites megalocarpa</i> (HOOK.f.) LANDER (syn. <i>Sonchus megalocarpus</i> (HOOK.f.) J. M. BLACK)	Cichorieae	AD; A.A. MUNIR 5512
2.	<i>Ainsliaea aptera</i> DC.	Pertyeae	KAL ; S. MUKHERJEE 25
3.	<i>Ainsliaea latifolia</i> (D. DON) SCH.BIP.	Pertyeae	KAL ; S. MUKHERJEE 17
4.	<i>Ainsliaea reflexa</i> MERR. var. <i>nimborum</i> HAND.-MAZZ.	Pertyeae	TAI; YUH FONG CHEN 3300
5.	<i>Arctium lappa</i> L.	Cardueae	Z ; Nr. 343
6.	<i>Arctotheca calendula</i> (L.) LEVYNS	Arctoteae	AD; N. N. DONNER 8541
7.	<i>Arctotis venusta</i> T. NORL.	Arctoteae	Z; Nr. 345
8.	<i>Baccharoides anthelmintica</i> (L.) MOENCH	Vernonieae	KAL; S. MUKHERJEE 1
9.	<i>Baccharoides calvoana</i> (HOOK.f.) ISAWUMI, EL-GHAZALY & B. NORD. ssp. <i>meridionalis</i> (WILD) ISAWUMI, EL-GHAZALY & B. NORD.	Vernonieae	SRGH; G. POPE 1930
10.	<i>Berkheya zeyheri</i> (SOND. & HARV.) OLIV. & HIERN ssp. <i>zeyheri</i>	Arctoteae	LISC; A.R. TORRE 6907
11.	<i>Bothriocline laxa</i> N. E. BR. ssp. <i>laxa</i>	Vernonieae	SRGH; M. MAVI 11
12.	<i>Carduus defloratus</i> L.	Cardueae	Z; Nr. 359
13.	<i>Carlina acanthifolia</i> ALL. ssp. <i>cynara</i> (POURRET ex DUBY) ROUY	Cardueae	Z; Nr. 360
14.	<i>Carlina vulgaris</i> L. ssp. <i>vulgaris</i>	Cardueae	Z; Nr. 361
15.	<i>Catananche caerulea</i> L.	Cichorieae	Z: Nr. 363
16.	<i>Centaurea cyanus</i> L. (syn. <i>Cyanus segetum</i> HILL)	Cardueae	Z; Nr. 364
17.	<i>Centaurea macrocephala</i> MUSS. PUSCHK. ex WILLD.	Cardueae	Z; Nr. 366

18.	<i>Centaurea maculosa</i> LAM. ssp. <i>maculosa</i>	Cardueae	Z; Nr. 369
19.	<i>Centrapalis kirkii</i> (OLIV. & HIERN) H. ROB.	Vernonieae	LISC; F.A. MENDONCA 2033
20.	<i>Cicerbita cyanea</i> (D. DON) P. BEAUV.	Cichorieae	KAL; S. MUKHERJEE 18
21.	<i>Cicerbita macrorhiza</i> (ROYLE) P. BEAUV.	Cichorieae	KAL; S. MUKHERJEE 19
22.	<i>Cirsium arvense</i> (L.) SCOP.	Cardueae	KAL; S. MUKHERJEE 23
23.	<i>Cirsium falconeri</i> (HOOK.f.) PETR.	Cardueae	KAL; S. MUKHERJEE 12
24.	<i>Cirsium japonicum</i> DC.	Cardueae	Z; Nr. 378
25.	<i>Cirsium vulgare</i> (SAVI) TEN.	Cardueae	BRI; s.n., s.coll.
26.	<i>Crepis pyrenaica</i> (L.) GREUTER	Cichorieae	Z; Nr. 383
27.	<i>Crepis vesicaria</i> L.	Cichorieae	AD; N.N. DONNER 8607
28.	<i>Echinops sphaerocephalus</i> L.	Cardueae	Z; Nr. 386
29.	<i>Elephantopus scaber</i> L.	Vernonieae	RB; SN 257
30.	<i>Gerbera jamesonii</i> BOLUS ex HOOK.f.	Mutisieae	Z, Nr. 397
31.	<i>Gymnanthemum amygdalinum</i> (DELILE) SCH.BIP. ex WALP. (syn. <i>Vernonanthura condensata</i> (BAKER) H. ROB.)	Vernonieae	RB ; SN 249
32.	<i>Hieracium villosum</i> JACQ.	Cichorieae	Z; Nr. 404
33.	<i>Hypochaeris glabra</i> L.	Cichorieae	AD; A. A. MUNIR 8601
34.	<i>Hypochaeris radicata</i> L.	Cichorieae	BRI; s.n., s.coll.
35.	<i>Lactuca dissecta</i> D. DON	Cichorieae	KAL; S. MUKHERJEE 43
36.	<i>Lactuca graciliflora</i> DC. (syn. <i>Stenosseris graciliflora</i> (WALL. ex DC.) C. SHIH)	Cichorieae	KAL; S. MUKHERJEE 52
37.	<i>Lactuca serriola</i> L.	Cichorieae	BRI; s.n., s.coll.
38.	<i>Launaea acaulis</i> (ROXB.) BABC. ex KERR	Cichorieae	KAL; S. MUKHERJEE 39
39.	<i>Launaea asplenifolia</i> (WILLD.) HOOK.f.	Cichorieae	KAL; S. MUKHERJEE 54

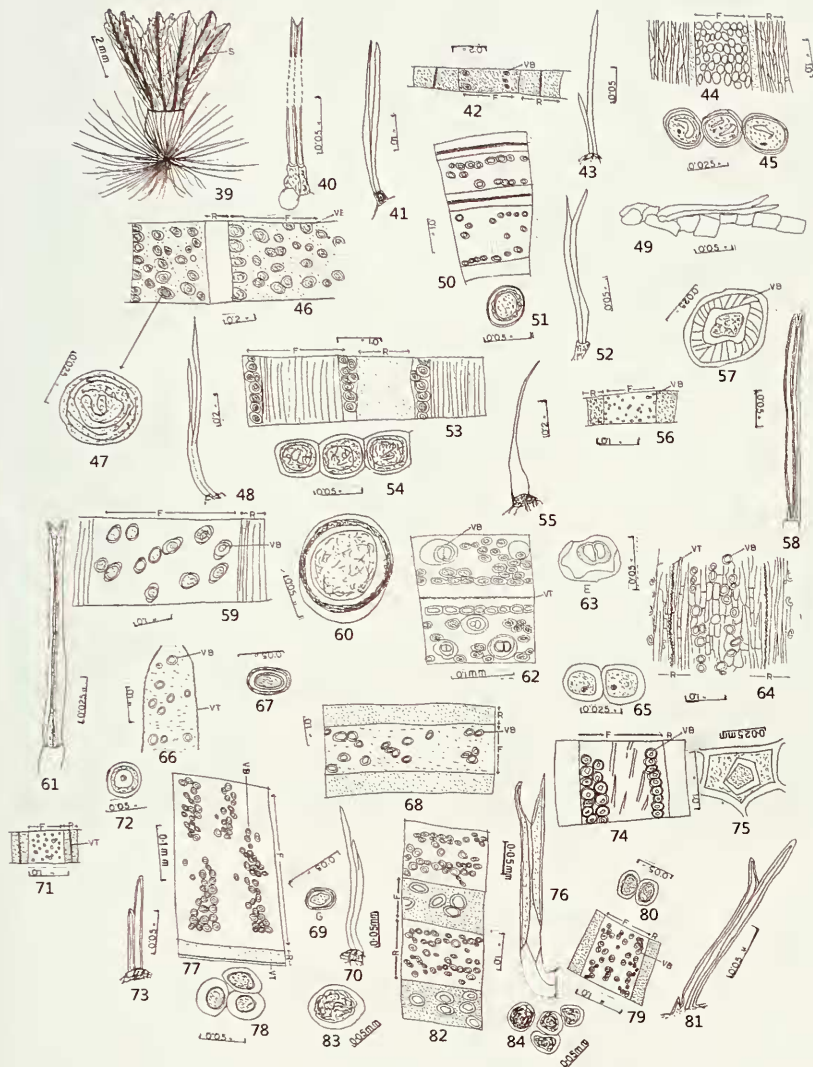
40.	<i>Launaea procumbens</i> (ROXB.) RAMAYYA & RAJAGOPAL	Cichorieae	KAL; S. MUKHERJEE 46
41.	<i>Launaea sarmentosa</i> (WILLD.) SCH.BIP. ex KUNTZE	Cichorieae	KAL; S. MUKHERJEE 37
42.	<i>Leibnitzia nepalensis</i> (KUNZE) KITAM.	Mutisieae	KAL ; S. MUKHERJEE 44
43.	<i>Lepidaploa gracilis</i> (KUNTH) H. ROB.	Vernonieae	RB; SN 250
44.	<i>Linzia melleri</i> (OLIV. & HIERN) H. ROB.	Vernonieae	LISC; R. SANTOS 2051
45.	<i>Macledium sessiliflorum</i> (HARV. in HARV. & SOND.) S. ORTIZ ssp. <i>sessiliflorum</i>	Dicomeae	LISC ; A. R. TORRE 13
46.	<i>Picris hieracioides</i> L.	Cichorieae	KAL; S. MUKHERJEE 29
47.	<i>Piloselloides hirsuta</i> (FORSSK.) C. JEFFREY ex CUFOD.	Mutisieae	KAL; S. MUKHERJEE 28
48.	<i>Polydora bainesii</i> (OLIV. & HIERN) H. ROB.	Vernonieae	SRGH ; G. POPE 1929
49.	<i>Polydora poskeana</i> (VATKE & HILDEBRANDT) H. ROB.	Vernonieae	LISC; A. R. TORRE & PAIVA 11332
50.	<i>Prenanthes khasiana</i> C. B. CLARKE	Cichorieae	KAL ; S. MUKHERJEE 67
51.	<i>Pseudelephantopus spicatus</i> (JUSS.) C. F. BAKER	Vernonieae	KAL; S. MUKHERJEE 21
52.	<i>Ptilostemon diacantha</i> (LABILL.) GREUTER	Cardueae	Z; Nr. 377
53.	<i>Rhaponticum scariosum</i> LAM. ssp. <i>rhaponticum</i> (L.) GREUTER (syn. <i>Leuzea rhapontica</i> (L.) J. HOLUB)	Cardueae	Z; Nr. 413
54.	<i>Rolandra fruticosa</i> (L.) KUNTZE	Vernonieae	RB; SN 255
55.	<i>Saussurea abnormis</i> LIPSCH. (syn. <i>Himalaiella abnormis</i> (LIPSCH.) RAAB-STRAUBE, should prob. be treated in <i>Jurinea</i>)	Cardueae	KAL; S. MUKHERJEE 32
56.	<i>Saussurea deltoidea</i> (DC.) SCH. BIP.	Cardueae	KAL; S. MUKHERJEE 22

57.	<i>Saussurea heteromalla</i> (D. DON) HAND.-MAZZ.	Cardueae	KAL; S. MUKHERJEE 27
58.	<i>Scorzonerooides autumnalis</i> (L.) MOENCH (syn. <i>Leontodon autumnalis</i> L.)	Cichorieae	Z; Nr. 409
59.	<i>Sonchus brachyotus</i> DC.	Cichorieae	KAL; S. MUKHERJEE 20
60.	<i>Sonchus schweinfurthii</i> OLIV. & HIERN	Cichorieae	SRGH; M. MAVI 8
61.	<i>Taraxacum officinale</i> WEBER	Cichorieae	AD; A. A. MUNIR 5500
62.	<i>Tarlmounia elliptica</i> (DC.) H. ROB., S. C. KEELEY, SKVARLA & R. CHAN (syn. <i>Vernonia elliptica</i> DC.)	Vernonieae	KAL; S. MUKHERJEE 57
63.	<i>Tragopogon porrifolius</i> L.	Cichorieae	AD; N. N. DONNER 8606
64.	<i>Vanillosmopsis capitata</i> (SPRENG.) SCH. BIP.	Vernonieae	RB; SN 248
65.	<i>Vernonanthura diffusa</i> (LESS.) H. ROB.	Vernonieae	RB; SN 254
66.	<i>Vernonia cinerea</i> (L.) LESS.	Vernonieae	KAL; S. MUKHERJEE 55
67.	<i>Vernonia cistifolia</i> O. HOFFM.	Vernonieae	SRGH; G. POPE 1931
68.	<i>Vernonia colorata</i> (WILLD.) DRAKE ssp. <i>colorata</i> (syn. <i>V. senegalensis</i> LESS.)	Vernonieae	LISC; SCHLIEBEN 2457
69.	<i>Vernonia glabra</i> (STEETZ) VATKE	Vernonieae	SRGH ; M. MAVI 12
70.	<i>Vernonia petersii</i> OLIV. & HIERN ex OLIV.	Vernonieae	LISC; A. R. TORRE 118
71.	<i>Vernonia scorpioides</i> (LAM.) PERS.	Vernonieae	RB; SN 251



Figs. 1–38. The structure and distribution of hairs from mature cypselas in different taxa.

- Figs. 1,2: *Gerbera jamesonii*.
Fig. 3: *Piloselloides hirsuta*.
Figs. 4, 5, 6: *Macledium sessiliflorum* ssp. *sessiliflorum*.
Fig.7: *Arctium lappa*.
Figs.8, 9: *Carlina acanthifolia* ssp. *cynara*.
Figs. 10, 11: *Carlina vulgaris* ssp. *vulgaris*.
Figs.12, 13: *Centaurea cyanus*.
Fig. 14: *Cirsium japonicum*.
Fig. 15: *Cirsium vulgare*.
Figs. 16, 17: *Echinops sphaerocephalus*.
Fig. 18: *Saussurea deltoidea*.
Figs. 1–9, 20: *Ainsliaea latifolia*.
Fig. 21: *Actites megalocarpa*.
Fig. 22: *Catananche caerulea*.
Fig. 23: *Cicerbita cyanea*.
Figs. 24–28: *Cicerbita macrorhiza*.
Fig. 29: *Crepis vesicaria*.
Fig.30: *Hieracium villosum*.
Fig. 31: *Hypochaeris glabra*.
Figs. 32, 33: *Hypochaeris radicata*.
Fig. 34: *Lactuca serriola*.
Fig. 35: *Scorzoneroide autumnalis*.
Fig. 36: *Taraxacum officinale*.
Fig. 37: *Tragopogon porrifolius*.
Fig. 38: *Arctiotheca calendula*.



Figs. 39–84. The structure and distribution of hairs from mature cypselas in different taxa.

Fig. 39: *Arctotis venusta*.

Fig. 40: *Berkheya zeyheri* ssp. *zeyheri*.

Fig. 41: *Baccharoides anthelmintica*.

Figs. 42, 43: *Baccharoides calvoana* ssp. *meridionalis*.

Figs. 44, 45: *Bothriocline laxa* ssp. *laxa*.

Figs. 46–48: *Centrapalis kirkii*.

Fig. 49: *Elephantopus scaber*.

Figs. 50–52: *Lepidaploa gracilis*.

Figs. 53–55: *Linzia melleri*.

Figs. 56–58: *Polydora bainesii*.

Figs. 59–61: *Polydora poskeana*.

Figs. 62, 63: *Rolandra fruticosa*.

Figs. 64, 65: *Vanillosmopsis capitata*.

Figs. 66, 67: *Gymnanthemum amygdalinum*.

Figs. 68–70: *Vernonanthura diffusa*.

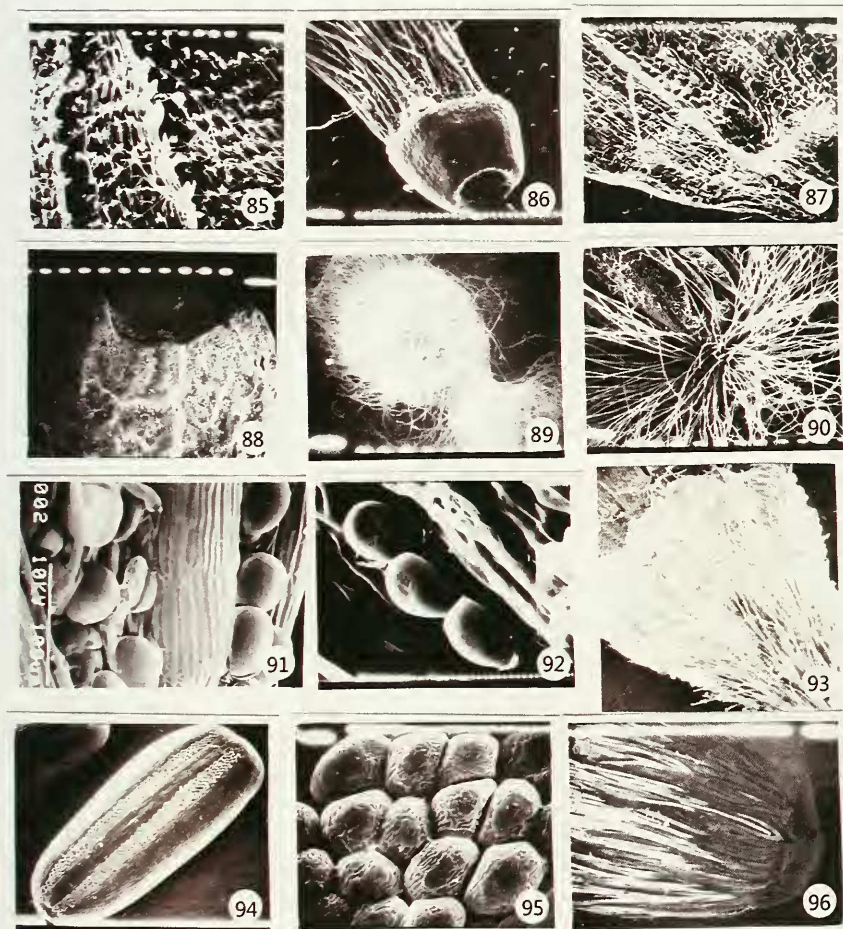
Figs. 71–73: *Vernonia cistifolia*.

Figs. 74–76: *Vernonia glabra*.

Figs. 77, 78: *Vernonia petersii*.

Figs. 79–81: *Vernonia scorpioides*.

Figs. 82–84: *Vernonia colorata* ssp. *colorata*.



Figs. 85–96. SEM photographs showing the structure and distribution of cypselar hairs.

Fig. 85: *Actites megalocarpa*, $\times 400$. Fig. 86: *Ainsliaea latifolia*, $\times 200$.

Fig. 87: *Ainsliaea reflexa*, $\times 100$. Fig. 88: *Arctium lappa*, $\times 50$.

Fig. 89: *Arctotheca calendula*, $\times 50$. Fig. 90: *Arctotis venusta*, $\times 50$.

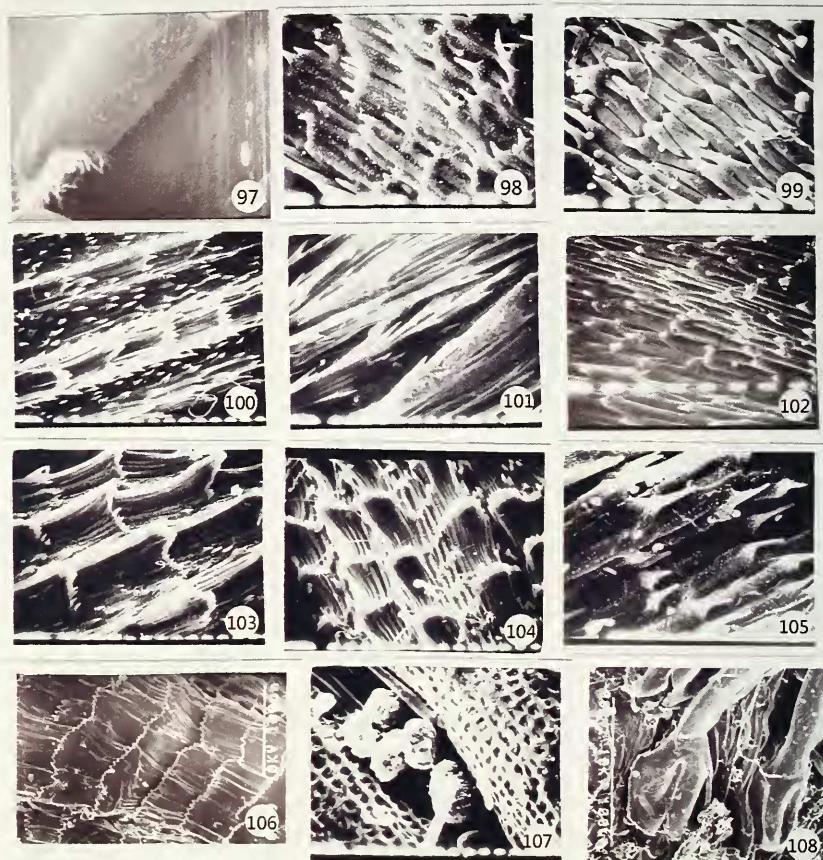
Fig. 91: *Baccharoides anthelmintica*.

Fig. 92: *Baccharoides calvoana* ssp. *meridionalis*, $\times 1600$.

Fig. 93: *Berkheya zeyheri*, $\times 50$.

Figs. 94, 95: *Bothriocline laxa*, $\times 100$; $\times 1600$.

Fig. 96: *Carlina acanthifolia*, $\times 100$.



Figs. 97–108. SEM photographs showing the structure and distribution of cypselar hairs.

Fig. 97: *Ceutaurea cyanus*, $\times 25$. Fig. 98: *Cicerbita cyanea*, $\times 800$.

Fig. 99: *Cicerbita macrorhiza*, $\times 800$. Fig. 100: *Crepis vesicaria*, $\times 400$.

Fig. 101: *Echinops sphaerocephalus*, $\times 400$. Fig. 102: *Hieracium villosum*, $\times 800$.

Fig. 103: *Hypochaeris glabra*, $\times 400$. Fig. 104: *Hypochaeris radicata*, $\times 400$.

Fig. 105: *Lactuca serriola*, $\times 1600$. Fig. 106: *Scorzoneroideis autumnalis*, $\times 400$.

Fig. 107: *Linzia melleri*, $\times 400$. Fig. 108: *Macledium sessiliflorum* ssp. *sessiliflorum*, $\times 400$.



Figs. 109–120. SEM photographs showing the structure and distribution of cypselar hairs.

Figs. 109, 110: *Polydora bainesii*, $\times 50$; $\times 400$. Figs. 111, 112: *Rolandra fruticosa*.

Fig. 113: *Sonchus brachyotus*, $\times 400$. Fig. 114: *Tragopogon porrifolius*, $\times 400$.

Fig. 115: *Vanillosmopsis capitata*, $\times 50$. Fig. 116: *Vernonia cistifolia*, $\times 800$.

Fig. 117: *Vernonia glabra*, $\times 200$. Fig. 118: *Vernonia petersii*, $\times 400$.

Fig. 119: *Vernonia scorpioides*, $\times 100$. Fig. 120: *Vernonia colorata* ssp. *colorata*, $\times 400$.

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